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A CARBONIFEROUS LABYRINTHODONT AMPHIBIAN WITH COMPLETE DERMAL ARMOR

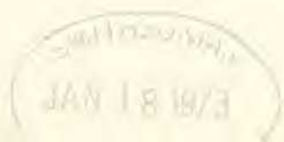
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ABSTRACT

Specimens of a labyrinthodont, *Greererpeton burkemorani*, from the Lower Carboniferous of West Virginia, show an apparently complete body covering of dermal scales, indicating the impossibility of "skin-breathing" in this early amphibian.

It has been suggested by many workers interested in the history of vertebrate respiration that skin-breathing was a transitional stage in the shift from gill-breathing in fishes to lung-breathing in higher terrestrial vertebrates. This hypothesis, of course, arises from the fact that in modern amphibians the skin is naked and moist and much of the oxygen-carbon dioxide exchange takes place through the skin. I have, however, recently (Romer, 1972) pointed out that such an evolutionary succession is highly improbable. To begin with, it is generally agreed that lungs were already present in the rhipidistian crossopterygian fishes from which land vertebrates quite certainly derived — fishes completely ensheathed in an armor of thick bony scales. However, an important question remains — what was the condition of the body covering in the ancient amphibians of the Paleozoic, from which the modern orders were derived? It could be argued that lungs, even if present in the ancestral tetrapods, may have been too primitive and ineffectual in nature to carry the whole burden of respiration, and that a naked skin may have been early called upon as a breathing aid. To evaluate properly the worth of such a concept, it is necessary to resort to paleontology and attempt to determine the nature of the skin in older amphibian types.



The living orders of amphibians — the Apoda (Gymnophiona), Urodela (Caudata), and Anura (Salientia) — are relatively modern groups. Almost nothing is known of fossils of the first group; urodeles go back only to the Cretaceous, last of the Mesozoic periods; frogs had developed by the mid-Mesozoic Jurassic Period, and one “pre-frog” (*Protobatrachus* or *Triadobatrachus*) is known from the Late Triassic. But amphibians originated far back, in Late Devonian times, and for the Late Paleozoic and even most of the Triassic Period — a stretch of time of close to one hundred and fifty million years — we find considerable faunas of amphibians, but amphibians quite distinct from the more modern types. Within these groups quite surely lay the ancestors of the later forms. What sort of body covering did these ancestors possess?

Two ancient groups have been advocated as possible ancestors — the Microsauria and the Labyrinthodontia. The microsaurians were small forms, usually but a few inches in length, whose remains are not infrequently preserved on slabs of shale which show not only the skeleton but also the nature of the skin. The skin is seen to have had a complete covering of bony scales; hence if the microsaurians were ancestors, the naked-skinned condition was surely a late acquisition.

However, current opinion (Parsons and Williams, 1963; Estes, 1965) favors the descent of the modern orders from the Labyrinthodontia, particularly the subgroup of this great order termed the Temnospondyli. The labyrinthodonts include a host of varied forms which were very prominent in Late Paleozoic and Triassic times. Some labyrinthodonts were small, but many ranged up to the size of a modern alligator or crocodile. For these forms, determination of the nature of the body covering is in general a matter of difficulty. Seldom are their remains discovered in flattened slab form, as are those of the little microsaurians. Usually they are found as three-dimensional burials in clays and shales. After death and before burial, the soft parts tended, of course, to rot, and skin as well as muscles and viscera were generally separated from the skeleton of the cadaver; further, excavation of the skeleton and its preparation in the laboratory has tended to do away with any remnants of the body covering of the living animal.

Almost invariably the ventral portion of the original fish-scale covering is retained in labyrinthodonts as a series of gastralia (or abdominal "ribs"), very useful in protecting the bellies of these low-slung animals (fig. 1). As regards the rest of the

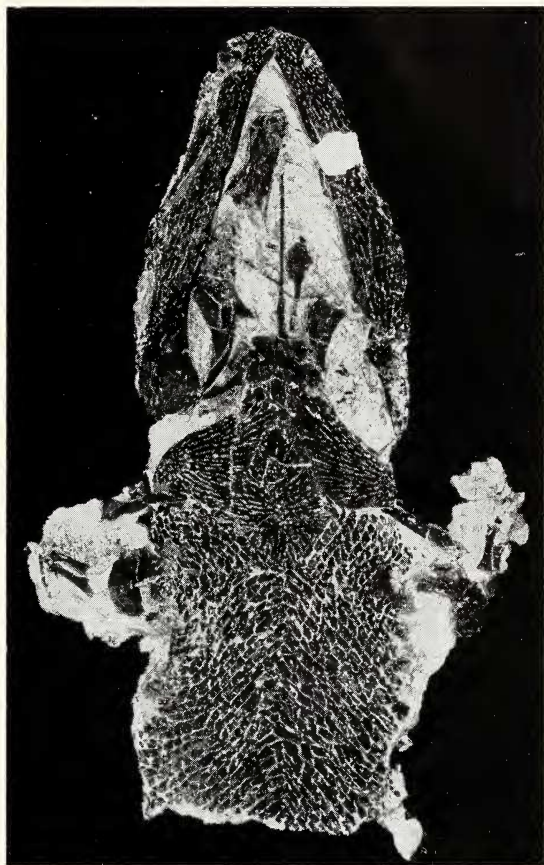


Fig. 1. Ventral view of head and part of trunk of a specimen of *Greererpeton*, CMNH 11090, showing the lower surface of the jaws, dermal shoulder elements and most of the ventral abdominal shield of gastralia. About 1/3 natural size.

body covering, knowledge is, as expected, meagre. As I noted in my recent paper (1972), dorsal squamation has been known in only four labyrinthodonts: *Eryops*, *Trimerorhachis*, *Archegosaurus*, and *Actinodon*. All four are temnospondylous labyrintho-

donts — the generic group from which the modern orders are very probably descended — but all four are, unfortunately, of relatively late (Permian) age. It would be of considerable interest to acquire data as to the nature of the body covering in the older members of the group.

As we descend the geologic scale, however, labyrinthodont remains become relatively rare. Numerous specimens have been found in the Upper Carboniferous — the Pennsylvanian Period of American nomenclature — but for the most part they represent forerunners of the Permian groups. From the entire Lower Carboniferous (Mississippian), there had been recovered, until recently, only a single rather poorly preserved labyrinthodont skeleton (*Pholidogaster*, Romer, 1964); a considerable amount of material of the oldest amphibians, the ichthyostegids, of the Late Devonian, has been collected but for the most part remains unstudied. We thus had very little knowledge of the structure of the older labyrinthodonts, and no adequate data upon which to judge the presence or absence of bony squamation in the most ancient members of the group.

This picture is now considerably altered by recent discoveries in the Mississippian of West Virginia. Most rocks of that age are marine in nature, but at Greer, near Morgantown, West Virginia, there occurs high up in the wall of a limestone quarry, a layer containing continental sediments (Hotton, 1970, p. 1-5). This layer is the Bickett Shale, a basal member of the Mauch Chunk Group, representing the upper portion of the Mississippian deposits of the area. In this shale there have been found for many years fragmentary remains of amphibians, and in the last few years the Cleveland Museum of Natural History has undertaken, under the direction of Dr. David H. Dunkle and with the assistance of William Hlavin and others, excavation of the bone layer there. Most of the bones are in a single layer exposed in the nearly vertical face of the quarry. Despite the difficulties of the task, the Cleveland Museum has already excavated to a variable depth (as much as 14 feet in one area) the main bone-bearing layer for some 50 feet along the quarry face. This layer proves to contain a nearly solid mass of amphibian remains, skulls and complete skeletons, closely packed and flattened dorso-ventrally so as to include, in essentially slab form, all the "hard"

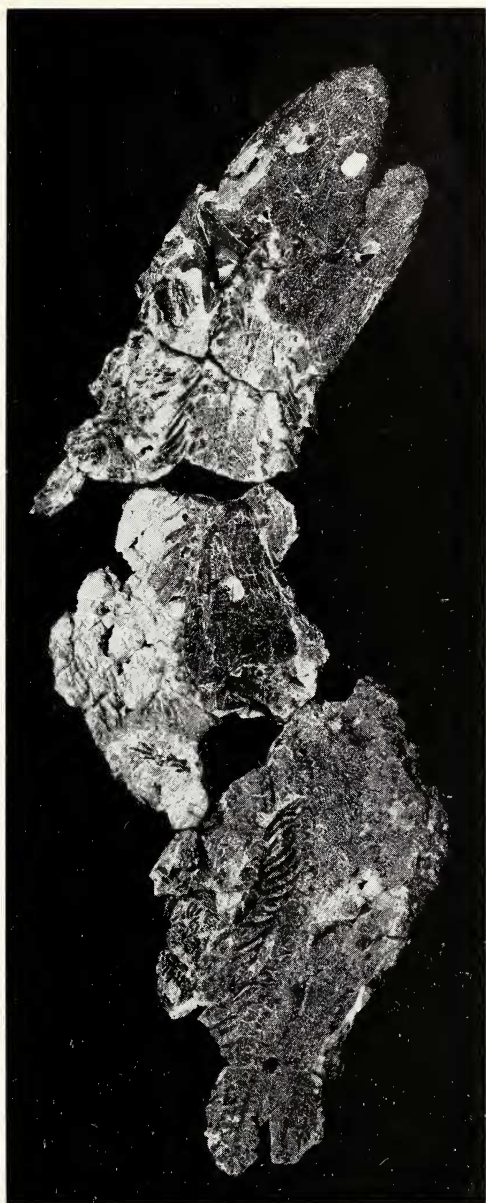


Fig. 2. Dorsal view of a slab containing much of the skeletons of three individuals of *Greererpeton* CMNH 11036, 11034 and 11082. Quantities of dorsal scales are visible, particularly posteriorly. About 1/6 natural size.

remains of the animal — not merely the skeleton, but also the skin if, in the process of burial, it had not been completely disintegrated and floated away from the main portion of the cadaver.

The most common amphibian in the bed is *Greererpeton*, a form of which I gave a preliminary description in 1969. The exact systematic position of this genus is at present none too certain. It is, however, a temnospondyl in vertebral structure and hence, in at least a broad sense, a member of the general group of labyrinthodonts from which modern orders are not improbably descended, although *Greererpeton* is certainly not in the direct ancestral line. In this genus the stout series of gastralia is to be found (fig. 1) covering the belly region. But in addition many of the specimens of this form show over the dorsal region a highly developed series of scales, subcircular in form and averaging 1.0 to 1.5 mm in diameter (figs. 2-4). The skin in which they were embedded in life had quite surely become more or less disintegrated before burial, and hence we cannot be sure of the exact nature of the scale pattern in life. It is, however, evident that even *post mortem* the disintegrating skin often retained a definite pattern of the arrangement of the scales in regular rows. There had rather certainly been a reduction in scale size from the situation seen in typical crossopterygians (cf. for example, Romer, 1966, fig. 100), and a lessening of the deep overlapping of scales seen in these ancestral forms; however, in some cases (cf. fig. 4) there are indications that a certain degree of overlapping persisted in the members of scale rows.

Rather surely the general body squamation in *Greererpeton* was not as complete as in crossopterygians, and some gaps may have existed between scales. But certainly the scale covering was such as to exclude the possibility of any great degree of skin breathing. It is, of course, not impossible to argue that some labyrinthodonts may have developed a naked skin. But the discovery of a well-developed scale covering in one of the oldest labyrinthodonts known, as well as evidence of a similar skin structure in a number of later temnospondyls, adds weight to the theory very generally accepted by paleontologists, that a scaled body sheathing was present in the ancestors of the modern



Fig. 3. Posterior portion of the block shown in figure 2, mainly skull and skeleton of CMNH 11082. Dorsal scales, preserved in more or less of a regular pattern, as seen along most of the region to the right of the vertebral column. Disarticulated gastralia are seen along the left margin. About 1/3 natural size.

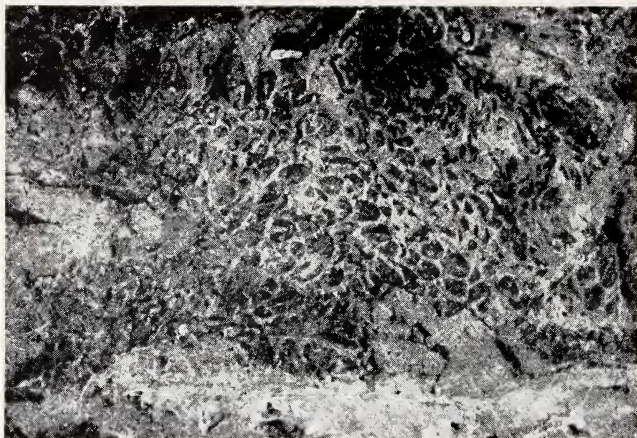


Fig. 4. A small portion of the dorsal region of a skeleton, CMNH 11070, about natural size, to show arrangement and possible overlapping of scales.

amphibians and that the development of a naked skin came about at a relatively late period in amphibian evolution.

Credit is due Virginia Heisey of the Cleveland Museum of Natural History for skillful preparation of the *Greererpeton* specimens, and to Bruce Frumker, of the same institution, for the excellent photographs from which plates 1-3 were derived.

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